A Revision of the Species of the Genus *Phyllodinarda* Wasmann with Notes on Their Behavior[1]

(Coleoptera : Staphylinidae)

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The genus *Phyllodinarda* was first described by Wasmann (1916: 105) to contain two species, *P. xenocephala* Wasmann from Cameroun and *P. kohli* Wasmann from the Congo Republic. In the same paper, he described the tribe Phyllodinardini to contain only this genus. In the original description of the genus, he compared it with the genus *Trilobitideus* Raffray and to the Cephaloplectinae. *Trilobitideus* was placed in its own subfamily, the Trilobitideinae in the same paper. Later (Wasmann, 1917: 328) he redescribed the genus and each of the two species as new again under the same names and then proceeded to a detailed morphological comparison of the genus with various genera, including *Dinarda* Mannerheim, *Rhoptrodinarda* Brauns, *Allodinarda* Wasmann, *Trilobitideus* Raffray, *Termitodiscus* Wasmann, *Discoxenus* Wasmann, and the tribes Trichopsenini and Termitopsenini. After doing all this, he came to the conclusion that *Phyllodinarda* was not very closely related to any of these and hence justified his inclusion of the genus in a tribe all by itself. There the matter has rested for some time. Bernhauer, Scheerpeltz, and Schubert (1926) recognized the tribe and placed it in their catalog almost 200 pages from the tribe Myrmedoniini to which it is probably most closely related and of which it is probably a member.

Students of the Coleoptera will recognize that the Cephaloplectinae was placed in the family Limulodidae by Seevers and Dybas (1943), and that Seevers (1965) has reduced the Trilobitideinae to a tribe, Trilobitideini, of the subfamily Aleocharinae. Also since Wasmann's time, *Rhoptrodinarda* and *Allodinarda* have been stated to be more closely related to *Zyras* Stephens than to *Dinarda* Mannerheim (Bernhauer, Scheerpeltz, and Schubert, 1926), thus placing them in the tribe Myrmedoniini. So the whole classification has shifted in such a way as to make a new study of the genus appropriate and to try to place it in relation to its Aleocharine relatives. The purpose of this paper is to redescribe and illustrate the generic characters of *Phyllodinarda*, to redescribe the old species and describe a new species, and to provide

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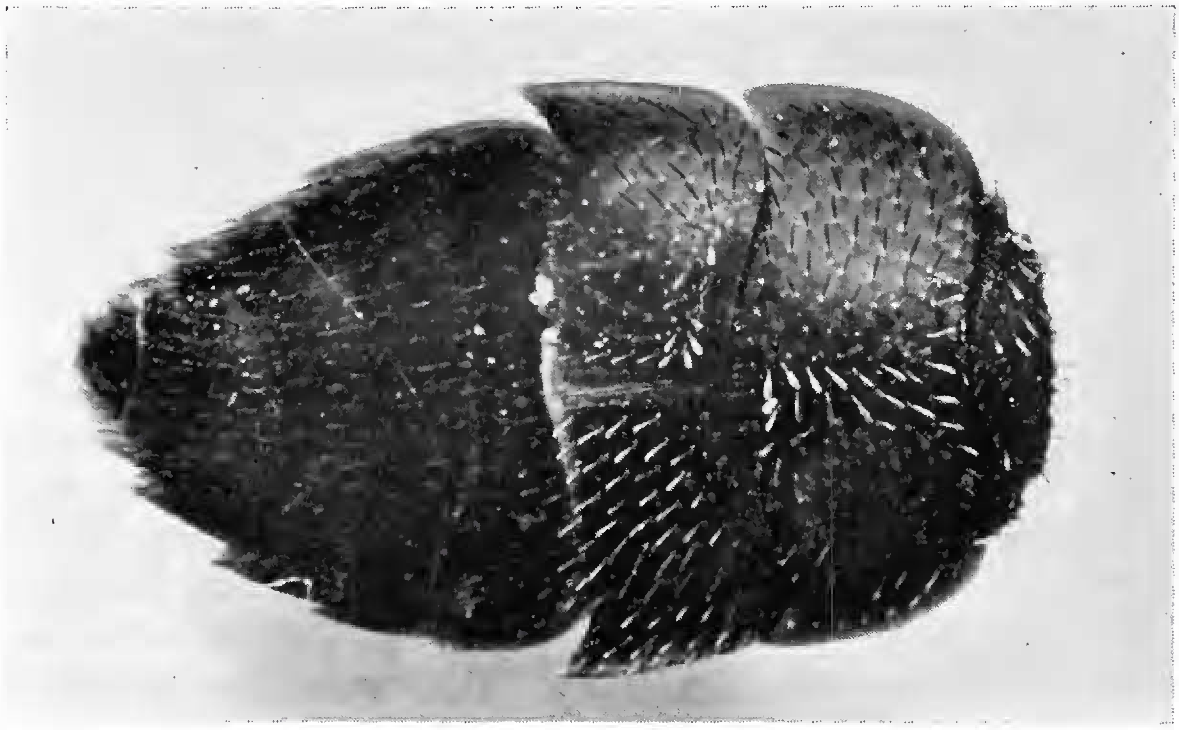
[1] This study was supported by a grant from the National Science Foundation (Grant NSF-GB-1366).

THE PAN-PACIFIC ENTOMOLOGIST 41: 121–131. April 1965

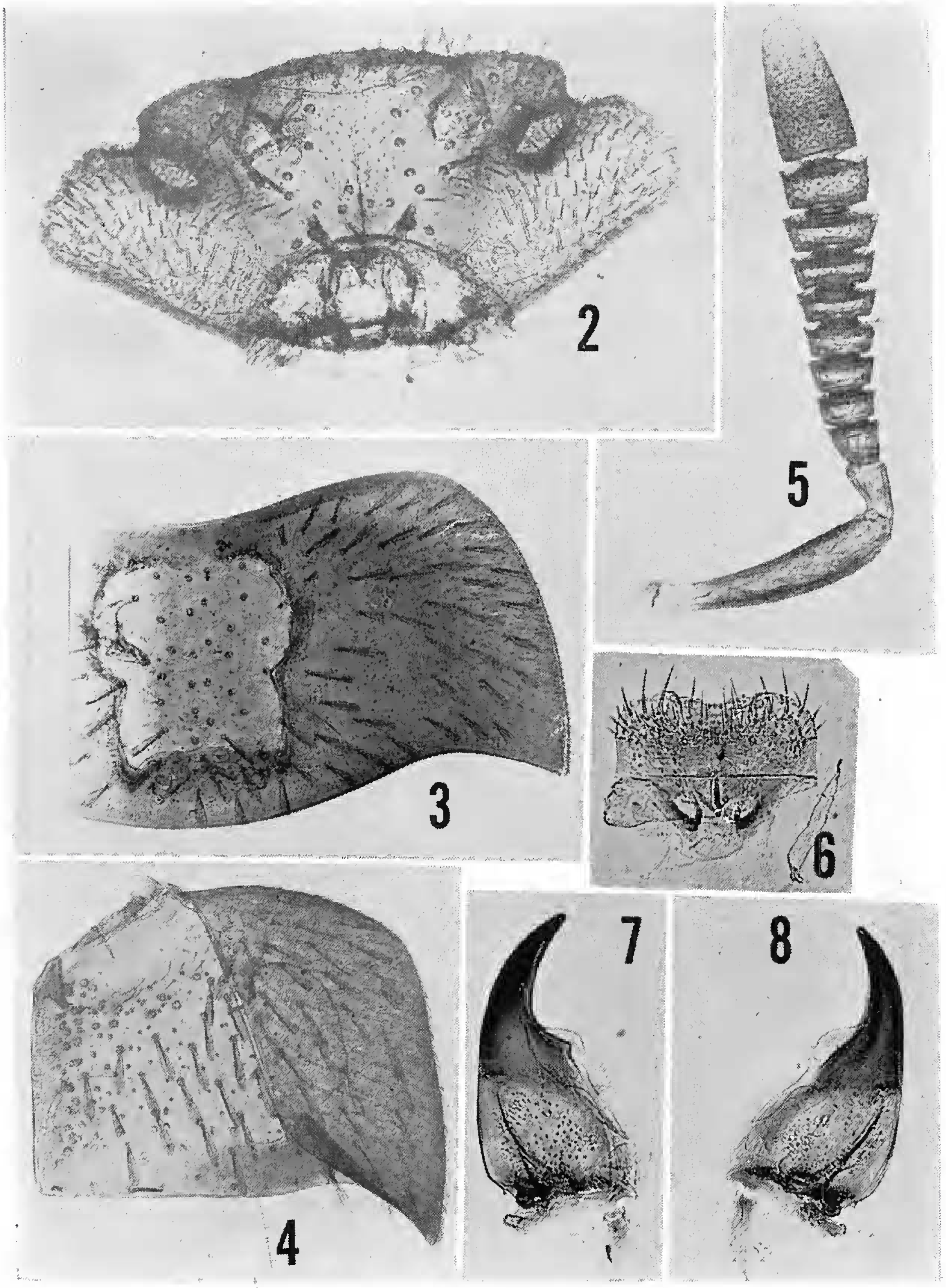


EXPLANATION OF FIGURE

Fig. 1. *Phyllodinarda kohli* Wasmann, dorsal aspect of whole animal. Photo taken with an Exacta XVIIa with a 50 mm lens at 32 cm of extension.

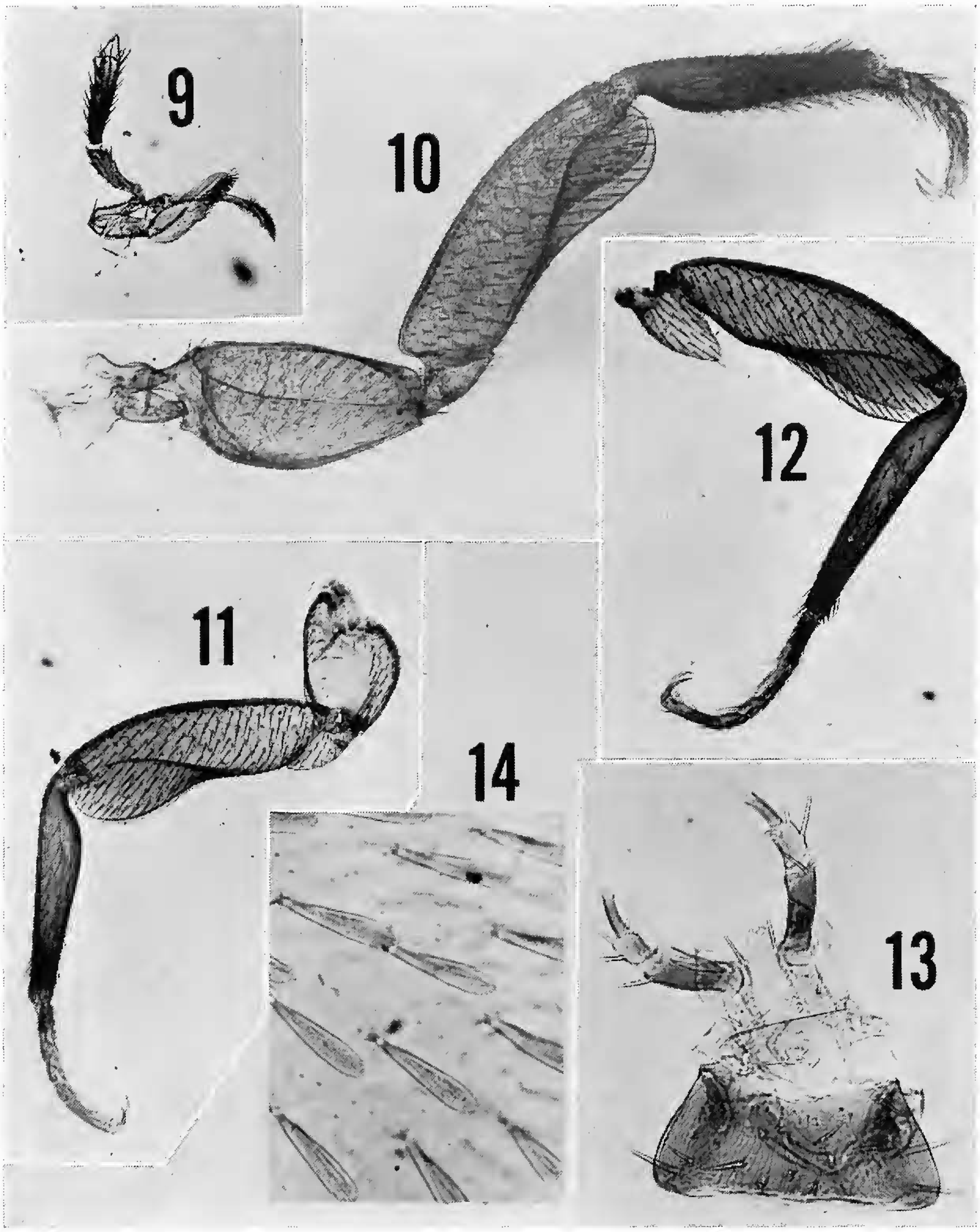
behavioral notes about the genus which provide some insight about its relations to its ant hosts.

Some of the specimens included in this paper were studied at the Chicago Natural History Museum (C.N.H.M.) where both Dr. Rupert L. Wenzel and Dr. Charles H. Seevers were helpful in allowing the investigator use of the collections and library of that institution. Other specimens were borrowed from the collections of the Musée Royal de l'Afrique Centrale, Tervuren (M.R.A.C.) for which I am grateful to M. P. Basilewsky, Curator and Chief of the Section of Entomology of that institution. Most of the specimens were collected by my wife, myself, and assistants in Africa, in which case they are in my collection (D.K.). The initials given above indicate the location of specimens cited. The ant hosts were determined for the material which we collected by Professor J. K. A. Van Boven, Université de Louvain. We are extremely grateful for these determinations. The assistance provided by Mr. Paul Edmiston and Mr. John Shower, Chico State College, in the preparation and dissection of material for study is also gratefully acknowledged. Certain concepts in the behavior section have been made clearer by discussion with numerous colleagues, but principally Professor Charles H. Seevers of Roosevelt University. However, any errors eventually uncovered are my responsibility as the advice of colleagues was not always followed.



Explanation of Figures

Figs. 2–8. *Phyllodinarda kohli* Wasmann: 2, head, ventral, mouthparts, and antennae removed; 3, pronotum, right half, dorsal, legs removed, 4, elytron, right dorsal; 5, antenna; 6, labrum; 7, right mandible; 8, left mandible. All microphotographs on this plate and the following were taken with a Leitz Orthomat Computerized Photomicrography Apparatus.



EXPLANATION OF FIGURES

Figs. 9–14. *Phyllodinarda kohli* Wasmann: 9, maxilla; 10, prothoracic leg; 11, mesothoracic leg; 12, metathoracic leg, without coxa; 13, labium; 14, details of spatulate setae on pronotum.

Genus PHYLLODINARDA Wasmann

Phyllodinarda Wasmann, 1916, p. 105; 1917, p. 329–349.

Type of the genus: *Phyllodinarda xenocephala* Wasmann, fixed by Blackwelder, 1952, p. 307.

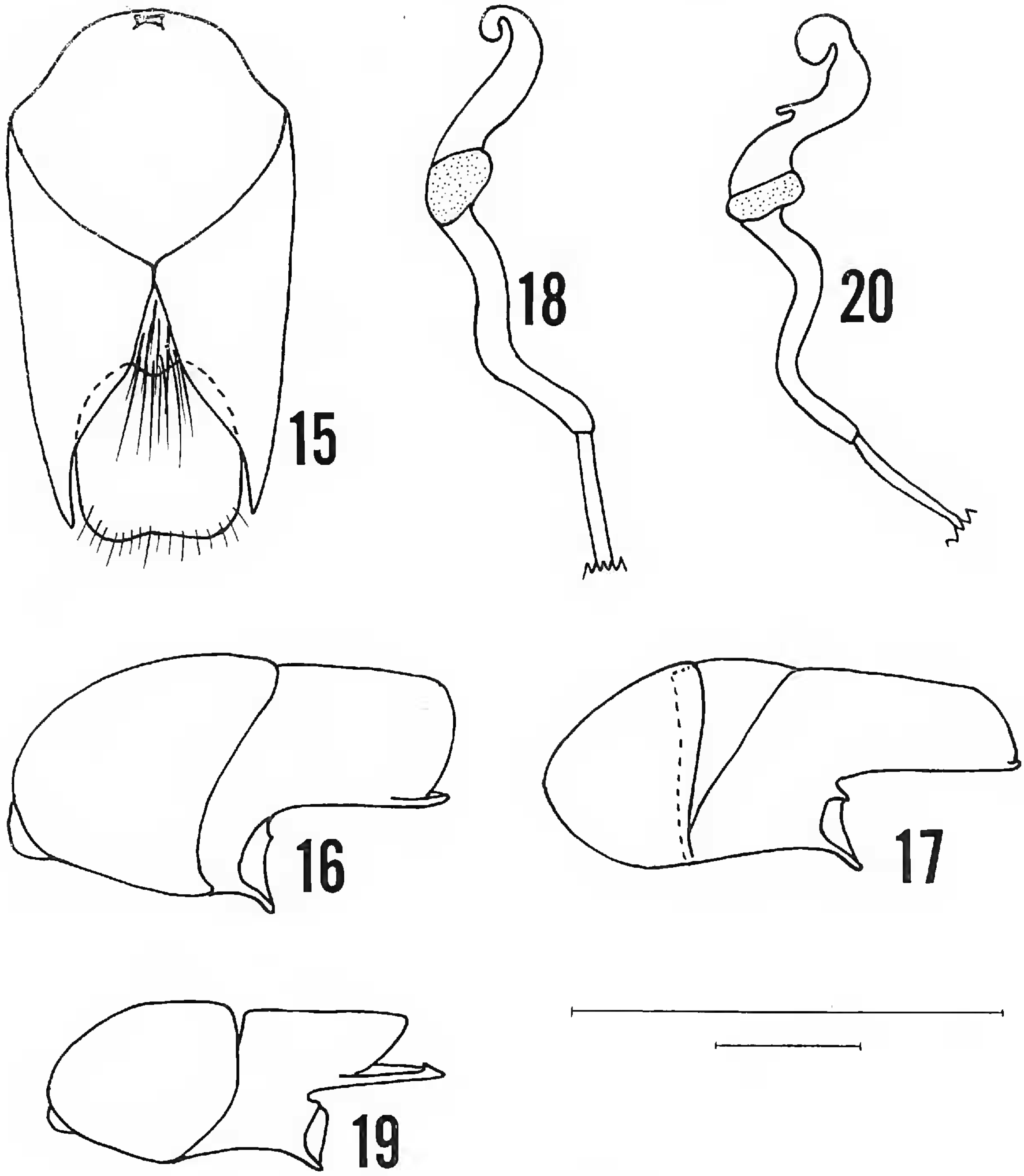
The genus is distinguished from all other staphylinid genera by many characteristics (see Fig. 1). The main problem has been to determine its relationships. Distinguishing characteristics include its very small, elbowed, and compressed antenna; its dorsoventrally flattened shape; its unique setae on the head, pronotum, elytra, and abdomen; and the way in which the eye has a ventral window.

Head triangular in shape, dorsoventrally flattened (Figs. 1 and 2). Gular sutures all but obliterated, with just a hint of a median line where the gula ought to be. Eyes directed forward along the narrow anterior axis with a ventral window so that certain facets are directed ventrally. Antennae reduced in size and inserted between the eyes on the ventral surface of the head. Antennae with a very large first segment which forms an elbow, rest of the segments strongly compressed with the lateral edges expanded so as to cover the petioles; 11-segmented; shaped as in Fig. 5. Labrum shaped as in Fig. 6. Mandibles are not symmetrical; left mandible shaped as in Fig. 8; right mandible shaped as in Fig. 7. Maxillae shaped as in Fig. 9; palpi 4-segmented. Labium shaped as in Fig. 13; palpi 3-segmented.

Pronotum dorsoventrally flattened and expanded laterally; shaped as in Fig. 3. Prosternum extremely small, subtriangular in form and fits in the median area shown in Fig. 3. Mesothoracic peritremes also extremely small but sclerotized. Elytra expanded laterally; shaped as in Fig. 4. Meso- and metasternum flat and without distinguishing features. Leg axis greatly shortened so that the legs do not usually protrude from under the pronotum and elytra and are hence usually invisible from the dorsal side. Proleg shaped as in Fig. 10. Mesoleg shaped as in Fig. 11. Metaleg shaped as in Fig. 12 with a flattened subtriangular coxa. The femora of all legs are expanded so as to form a shield for the tibiae in repose. Tarsal formula, 4–5–5.

Abdomen dorsoventrally flattened and expanded laterally. Overall shape as in Fig. 1. Two pairs of paratergites on segments III–VI, one pair of segment VII. The pairs of paratergites are extremely wide on segment III, each pair on each side making up about ⅕ of the total width of the segment. The width of these paratergites narrows drastically on each succeeding segment contributing greatly to the posterior tapering of the abdomen. Segment VIII without paratergites. Segment IX without paratergites and shaped as in Fig. 15. The anterior edge of the sternite of segment IX is evenly rounded in females (as in the figure) but contains a long process on each side in males. Tergite VII with a tergal gland at the midline. Male genitalia tubular, variable by species. Spermatheca of female with a sclerotized tip leading to a long many coiled but not twisted spermathecal duct. The sclerotized tip of this is variable by species whereas the coiled portion does not appear to vary.

The whole dorsal surface of the animal and the ventral surface of the head contains two kinds of setae. One kind is not unusual as they are found on many staphylinids. These are best seen in the photos of the legs (Figs. 10, 11, and 12) but are also to be seen on the photos of the head, pronotum, and elytra. The other kind is a large spatulate seta which can be seen in the photos of the head, pronotum, and elytra. This seta



EXPLANATION OF FIGURES

Figs. 15–20. *Phyllodinarda kohli* Wasmann: 15, 9th abdominal segment, female, dorsal view; 17, median lobe of the male genitalia; 18, spermatheca, coiled spermathecal duct removed. *P. xenocephalla* Wasmann: 16, median lobe of male genitalia. *P. alzadae* Kistner: 19, median lobe of the male genitalia; 20, spermatheca, coiled spermathecal duct removed. Each scale represents 0.25 mm. The larger scale refers to Figs. 18 and 20, while the smaller applies to all other figures.

emerges from a puncture which penetrates the exoskeleton. Each seta has a hollow tube running through it which emerges at the apex and when enlarged (Fig. 14) can be seen to have a fimbriated tip. Wasmann (1917) showed that there were gland cells underneath the skeleton at the base of these setae. Our investigations confirm this. The ventral surface of the abdomen, and the ventral surface of the thorax does not contain the spatulate type of setae but does contain the more usual kind of setae.

RELATIONSHIPS.—This genus has many specialized features which are unique to it and have obscured its relationships for many years. If the specialized head shape and the unique setae are ignored, then many resemblances of the genus to *Zyras* (*Batsa*) Blackwelder (= *Watsa* Bernhauer) are seen. The latter should probably be a genus instead of a subgenus. However, only two or three specimens have ever been captured and a detailed comparison will have to await more specimens. Only the characteristics which, in my opinion, place it in the tribe Myrmedoniini are listed: (1) Mouthparts: Labium and labrum closely approximate those of *Zyras* (*Aulacocephalonia*), *Myrmechusa*, and other Myrmedoniini. The maxilla has the extra long galea which also approximates all other Myrmedoniini. (2) Legs: Coxal structure with the short internal processes. Tarsal formula, 4–5–5. (3) Abdomen: Shape of the abdominal segment IX complex, even to the sexual difference of the anterior border. Highly coiled spermathecal duct with a sclerotized spermatheca. Tergal gland on abdominal segment VII.

Any of these characteristics taken individually would not define the Myrmedoniini but when they are considered as a group, they adequately define the Myrmedoniini. The species present a rather uniform external appearance. *P. kohli* is a little larger on the average but small specimens are caught and these fall within the range of the other two species. The easiest way to determine them is to dissect out the genitalia and compare them with the figures. In the field, a generic determination plus a locality is about all that can be done.

PHYLLODINARDA XENOCEPHALA Wasmann

(Fig. 16)

Phyllodinarda xenocephala Wasmann, 1916, p. 107, Plate 3, fig. 4 (Cameroun: Grand Batanga, with *Dorylus* (*Anomma*) *nigricans* ssp. *sjoestedti* var. *rufescens* Wasmann, Coll. G. Schwab; Lolodorf, Coll. Miss Makenzie); 1917, p. 330, plate 9, figs. 35 and 36 (same data); Mann, 1922, p. 628 (Cameroun: Akono-Olinga, with *D.* (*A.*) *nigricans* ssp. *sjoestedti* Emery).

Distinguished from all other species by the shape of the median lobe of the male genitalia.

Color varies from light reddish brown to dark reddish brown. Head somewhat darker than the rest of the body. Dorsal surface of the entire animal glistening underneath the mat of spatulate and pointed setae. Median lobe of the male genitalia shaped as in Fig. 16. Spermatheca unknown.

Measurements.—Protonum length, 0.93–1.00 mm; elytra length, 0.55–0.66 mm. Number measured, 4.

MATERIAL EXAMINED.—Cameroun: 2, with no further locality data, Coll. Thaxter (C.N.H.M.); 1, Akono-Olinga, with *Dorylus* (*Anomma*) *nigricans* ssp. *sjoestedti* Emery, Coll. G. Schwab (C.N.H.M.); 1 male, Edéa, 27 July 1962, from the end of a raiding column of *D.* (*A.*) *nigricans* ssp. *sjoestedti* var. *rufescens* (Wasmann) Emery, nest No. 85, Coll. D. H. Kistner (D.K.).

PHYLLODINARDA KOHLI Wasmann

(Figs. 1–15, 17–18)

Phyllodinarda kohli Wasmann, 1916, p. 107 (Congo Republic, St. Gabriel near Stanleyville, 20 August, 29 August 1910, with *Dorylus* (*Anomma*) *wilverthi* Emery, Coll. P. H. Kohl); 1917, p. 330, Plates 9 and 10, figs. 37–51 (same data, added that the specimens were taken from the end of a raiding column).

Color varies from a light reddish brown to dark reddish brown. Head usually a little darker than the rest of the body. Dorsal surface of the entire body glistening underneath the mat of spatulate and pointed setae. Median lobe of the male genitalia shaped as in Fig. 17. Spermatheca shaped as in Fig. 18.

Measurements: Pronotum length, 1.00–1.15 mm; elytra length, 0.65–0.70 mm. Number measured, 10.

MATERIAL EXAMINED.—Congo Republic: 2, Cotypes, *P. kohli* Wasmann, det. E. Wasmann, St. Gabriel near Stanleyville, 20 August 1910, with *Dorylus* (*Anomma*) *wilverthi* Emery, Coll. P. H. Kohl, (C.N.H.M.); 1, Cotype, *P. kohli* Wasmann, det. E. Wasmann, same data but lacking a date (C.N.H.M.); 1, Stanleyville, Coll. Fr. Majelka (C.N.H.M.); 1, Yangambi, March 1955, with ants, (Coll. J. Décelle) (M.R.A.C.); 29 (12 males, 11 females), Yangambi, 2 July 1960, from the end of an emigration column of *D.* (*A.*) *wilverthi* Emery, nest No. 19, Coll. D. H. and A. C. Kistner and R. Banfill, (D.K.); 1 female, Yangambi, 3 July 1960, from the end of a raiding column of *D.* (*A.*) *wilverthi* Emery, nest No. 24, Coll. D. H. and A. C. Kistner and R. Banfill (D.K.); 2 males, 9 July 1960, from the end of a raiding column of *D.* (*A*). *nigricans* ssp. *sjoestedti* var. *rufescens* (Wasmann) Emery, nest No. 35, Coll. D. H. and A. C. Kistner and R. Banfill (D.K.).

Phyllodinarda alzadae Kistner, new species

(Figs. 19–20)

Color varies from light reddish brown to dark reddish brown. Head darker than the rest of the body. Dorsal surface of the entire body glistening underneath the mat of spatulate and pointed setae. Median lobe of the male genitalia shaped as in Fig. 19. Spermatheca shaped as in Fig. 20.

Measurements: Pronotum length, 0.96–1.05 mm; elytra length, 0.65–0.68 mm. Number measured, 6.

Holotype.—female, No. 11328, Uganda, Kisubi Forest near Entebbe, 19 July 1960, from the end of an emigration column of *Dorylus* (*Anomma*) *wilverthi* Emery, nest No. 37, Coll. D. H. and A. C. Kistner and R. Banfill (D.K.). Paratypes: 5 (4 males), same data as holotype.

Behavior of the Species

All records of all the species show that the specimens were only seen at the ends of raiding and emigration columns. We never saw them in the central parts of any columns. This indicates that these myrmecophiles do not participate in the raiding and emigration aspects of colonial behavior. They would therefore fall into the category of what I have called the nonintegrated groups.

All groups of myrmecophiles, at least as far as those concerned with Driver Ants in Africa are concerned, fall into two general categories. The integrated groups are those that participate in the raiding and emigration activities of the colony and are thus seen in the columns at all times except perhaps when the ants are at their highest level of excitation, namely at the raiding head. Two staphylinid groups make up the majority of the integrated forms, namely the Pygostenini and the Dorylomimini. The Dorylomimini are morphological mimics of the ants and achieve integration by means of passing antennal scrutiny by the ants. The Pygostenini are what I have called primarily behavioral mimics in that they fold their abdomens (the tips of which are morphologically narrowed) over their backs when in contact with the ants and thus present an ant-like "appearance" to the antennae of the ants. Both groups have evolved phoretic members from ancestral types which had these basic modifications. The Dorylomimini has evolved one genus, *Dorylocratus Wasmann* (Kistner 1964), which has secondarily evolved a glandular abdomen. The glands of the females are attractive to worker ants. The basic modification (morphological or behavioral mimicry) has been evolved independently in at least two other staphylinid groups in Africa but on a limited basis both host-wise and geographically. All of this has been documented in a series of papers which are in various stages of completion. The whole concept of integrated myrmecophily can thus be viewed as adaptations to the predominant integrating mechanism of the society. In African Driver Ants, where trophallaxis is poorly developed at best, and sight is nonexistent among both queens and workers, antennal palpation seems to play a dominant role and thus the majority of the integrated myrmecophiles "feel" like ants. In many North American and European ants, as well as termites, trophallaxis appears to play a more dominant role and the myrmecophiles and termitophiles display more glandular development.

The nonintegrated forms are represented by an even larger number of myrmecophiles, each genus of which has its own story or series of adaptations to the ant colony. When the whole picture is gradually assembled, we shall see a whole series of relationships from facultative predation to obligate predation, from facultative scavenging to obligate scavenging with quite a few of the different groups of Staphylinidae and other insects involved and with phylogenetic series representing progressive degrees of adaptation. The detailed analysis of these interrelationships, both phylogenetic and ecologic, has just been started with the description of the behavior of *Myrmechusa* Wasmann (Koblick and Kistner, 1965) as the first completed work.

In *Phyllodinarda* then, we have a nonintegrated genus with a whole series of structural modifications which are perhaps more bizarre than those of many integrated forms. We attempted in the field to determine how the beetle uses these.

The following protocols have been extracted from our field notes on *Phyllodinarda kohli* Wasmann in Yangambi, Congo Republic, 2 July 1960. The end of the emigration column that we sampled on the previous day commenced about 8:00 o'clock in the morning. Among literally thousands of myrmecophiles that streamed by, the *Phyllodinarda* were very noteworthy. Most of the specimens (18 of 29) streamed by during the first hour of observation and collecting. They have a "halt, take cover, and proceed" kind of gait. They lurked under blades of grass, dead leaves, and twigs along the trail, then when they detected a break in the activity they would lumber along for awhile and then take cover again. Twice we saw an ant move toward a *Phyllodinarda* whereupon the *Phyllodinarda* would depress itself against the ground. When it did this, in each instance we saw the worker ant approach the beetle and move its mouthparts and antennae over the dorsal surface. After a brief instant of this, the ant pulled back and departed. We attempted to smell the beetle but no odors were detectable either in the air or in the aspirator when the beetle was captured, although it was apparent that the ant was repelled.

Protocols on the other species yield no new data, although we did see one more ant–beetle encounter as described above for *P. alzadae* Kistner. For the Kisubi captures (*P. alzadae*), we noted the manner of walking which consists of each tagma raising and lowering in sequence and thereby producing a dorsoventral undulating appearance. We were not fortunate enough to see them eating, and stomach analysis yielded nothing that was identifiable. *Phyllodinarda* is probably either an obligate predator or scavenger associated with driver ants since they have never been captured in any other situation. Because it follows so closely upon the end of the column where there are straggler ants, we are inclined to the view that it is a predator. The scavengers are typically farther away from the ants or making their way between the small dirt particles of the trail roadway. Its method of eluding stray ants consists of the obvious avoiding reaction in hiding under debris along the trail and proceeding when there are few ants passing. However, its legs are so short and it is so slow that chance encounters with ants seem to be not infrequent. When an encounter occurs, its depression on the ground may prevent the ant from picking it up, but this I doubt because the ants are quite capable of picking up similarly shaped insects such as roaches which are a regular feature of their diet. The dorsoventral compression when depressing on the ground may squeeze the products of the glands at the base of the hollow spatulate setae up through the setae. This the ant finds unattractive and hence pulls back away from the beetle.

In his analysis, Wasmann (1917) considered the genus to be a "*Vertreter des extremsten Trutztypus*" (a representative of the extreme defensive form). It is hard to conceive how the flattened form could serve to protect this insect from the ants, but the shortening of the legs and antennae as well as the compression of the antennomeres could have a protective value. In any event, the concept of a specially adapted predator or scavenger with an obligate relationship to driver ants is an idea that has wider currency in biology and describes its situation better than the word synoeckete or synecthran.

The records from Cameroun for *P. xenocephalla* and from the Congo for *P. kohli* indicate that host specificity applies only at the subgeneric level.

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SCIENTIFIC NOTE

A new locality record of *Mohavacris timberlakei* Rehn, at Bishop, Inyo County, California (Orthoptera : Tanaoceridae).—*Mohavacris timberlakei* was described in 1948 from a unique male specimen captured near Highway 138, Mohave Desert, California, 3,600 feet elevation (Edith M. Timberlake, 20 April 1947), probably a few miles east of Llano near the course of Rock Creek wash. Additional specimens have since been captured by Grant, Helfer, Hubbell, Rentz, and Tinkham in the near vicinity and as high as 5,750 feet at Cactus Flat in the San Bernardino National Forest on Highway 18. Rentz has taken specimens from the Cajon Pass area well after dark on *Artemisia tridentata.* We were surprised to find a male of this rare species from a fluorescent black light trap at Bishop in April of 1964. The trap, operated by Mrs. Ruth Keleman, was situated on a porch 3 feet above ground level. The trap rim, an additional 3 feet high, was successfully negotiated by this strong jumper. After the capture, the trap was placed among the native vegetation and, although a diligent search was made, no additional specimens were found or taken in the trap. Bishop has an average rainfall of 5 inches annually and is about 4,500 feet above sea level. This capture suggests the possibility of the discovery of additional specimens of *Mohavacris timberlakei* from within, and areas immediately surrounding, the Mohave Desert.

Mohavacris timberlakei is not known to be sound producing; however, Rentz states that *Tanaocerus*, the other known genus of the family, will drum upon a branch and make a knocking sound.—G. M. BUXTON, *California Department of Agriculture, Sacramento.*